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Observations on Burrowing Behavior in *Limulus polyphemus* (Chelicerata, Merostomata), with Implications on the Functional Anatomy of Trilobites

BY NILES ELDREDGE¹

INTRODUCTION

The functional significance of many structures described in trilobites is obscure. Although most of the blame lies in the usual nonpreservation of the crucial ventral structures (especially the appendages) necessary to make the basic inferences on mode of life, many known structures have yet to be fully explained in a functional sense. One possible course of action on such problems is the comparison of trilobites with other arthropods that are either closely related and morphologically similar because of parallelism or unrelated and morphologically similar because of convergence.

The only living North American representative of the Merostomata, *Limulus polyphemus* L., has much to recommend it as a possible model for the interpretation of some of the anatomical peculiarities of trilobites. For one thing, there is a general, though not universal, feeling that chelicerates and trilobites are more closely related to each other than either is to crustaceans, even though the trilobites or their immediate precursors

¹ Assistant Curator, Department of Invertebrate Paleontology, the American Museum of Natural History.

may have given rise to both groups. Of perhaps greater importance than sheer propinquity of descent is the apparent similarity in over-all external carapace morphology, in basic locomotory and, to a certain degree, feeding mechanisms between the merostomes and trilobites; although the feeding mechanisms of such branchiopods as the notostracan *Triops* Shrank have been used recently to elucidate the functional morphology of feeding in certain trilobites (Eldredge, In press), there are greater similarities in limb structure and cephalic shape between *Limulus* and certain trilobites than there are between most trilobites and crustaceans. Similarly, arachnids, especially scorpions, claim virtually as close a degree of phylogenetic affinity to trilobites as do xiphosurid merostomes, but here again modifications in feeding (suctorial) and locomotion (terrestrial) in arachnids beclouds any comparison with trilobites.

It is always easy to overdo an analogy, and caution must be exercised when an obviously specialized animal such as *Limulus* is taken as a model for interpretation of trilobites. After all, great differences in morphology exist between the groups, the most obvious being in the composition of tagmata and in gill structures. But the primary rationale underlying use of *Limulus* as a model lies in the essential similarity of its locomotory mechanisms to those of trilobites. The walking legs in the two groups are closely comparable and in all likelihood these legs (telopodites) in trilobites had a promotor-remotor swing in walking as in *Limulus* (see Manton, 1963, p. 131-136). Short of dredging a living trilobite from the abyssal plains, and keeping in mind xiphosurid modifications that have no bearing on trilobite morphology, a study of *Limulus* could go far toward the elaboration of the correct interpretation of many features of trilobite anatomy.

Most of the present study is devoted to anatomical aspects of the tergite of *Limulus* involved in burrowing. The investigation was undertaken with the hope of shedding light on the function of the micro-tubules that perforate the tergal carapace of many trilobites. In addition, some trilobites possess peculiarities in prosomal morphology reminiscent of the condition in *Limulus*, which possibly reflect similar adaptations.

ACKNOWLEDGMENTS

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ABBREVIATION

A.M.N.H., Department of Invertebrate Paleontology, the American Museum of Natural History

MATERIALS AND METHODS

Seven sexually immature specimens of *Limulus polyphemus* transported to the University of California, Berkeley, from somewhere on the east coast of North America, where they occur from Nova Scotia to Mexico, were used in the present study. Table 1 gives some basic dimensions of the animals. The specimens had been living in a sea table at the Bodega Marine Laboratory (University of California) without food or accustomed substratum for at least three weeks before they were placed in an aquarium with a 5-inch thick substratum of medium-fine quartz sand and fed errant polychaetes and crushed *Macoma nasuta* Conrad, a soft-shelled clam. The seven animals remained in the aquarium for 10 days prior to the start of detailed observations, and although both temperature and salinity may have been lower in the aquarium than in the preferred native habitat, the specimens appeared far more vigorous after being "revived" in the tank and remained quite active up to the termination of the project.

The seven specimens of *Limulus* were numbered with a standard glassware crayon. Setae were cemented to the carapace with Superba Cal Mix—a hydro-phosphate dental cement manufactured by Superbadental Products, Japan. The most effective results were obtained by drying the area of the carapace to be coated, then using a very viscous preparation of the cement. The cement had little affinity for the chitin surface of the carapace and tended to flake off when rubbed against sand particles.

All observations on burrowing were made in the one aquarium; details

TABLE 1
BASIC DIMENSIONS OF SPECIMENS OF *Limulus polyphemus*
(Measurements are in sixteenths of an inch)

Specimen Number	Sagittal Length of Prosoma	Width Between Eyes	Width Between Genal Angles	Sagittal Length of Opisthosoma	Sagittal Length of Telson
1	33	22	43	15	38
2	34	26	44	20	21
3	32	25	41	18	39
4	34	24	45	17	33
5	38	27	50	19	45
6	23	15	37	12	29
7	31	21	42	17	40

of procedure and experimental design are included in the appropriate places below.

BURROWING STAGES IN *Limulus polyphemus*

Limulus polyphemus is a predominantly nocturnal species that spends the daylight hours completely covered with a thin layer of substratum, usually coming to the surface to scavenge only at night (Lochhead, 1950, p. 361). After an initial 24-hour "revival" period spent in adjusting to tank conditions, any specimen removed from its burrow and placed on the surface of the substratum immediately began to rebury itself. The burial process in each of the seven specimens was watched several times to arrive at a composite picture of burrowing behavior and mechanisms; actually, there was little variation in behavior both within and among specimens.

Figure 1 shows the anatomical features referred to in the description of the burial process. The process is begun (Stage 1) by a downward flexion of the prosoma on the opisthosoma—a procedure more fully analyzed below. The opisthosoma is kept in a more or less horizontal plane throughout the process. A symmetrical wall of sand is pushed up the steep slope of the anterior margins of the prosoma, reaching the eyes and the genal angle at the same time; the prosoma is flexed back to the horizontal position at this time, the animal moves forward, and the wall of sand is spread back along the horizontal central portion of the prosoma. The prosoma may be flexed down again to insure a sufficient supply of sand to cover the entire prosoma.

Locomotion during Stage 1 is effected by promotor-remotor action of the walking legs, and by movement of the telson in the horizontal plane only. The telson is thus always buried. The medial marginal areas of the opisthosoma are passively buried by sand falling off the posterior lateral margins of the prosoma. Stage 1 ceases when the opercular pleurite (the distally unfused portion of the hemi-segment 8—see Snodgrass, 1952, p. 25, fig. 7 and fig. 1, present paper) on the opisthosoma is covered. The channel (fig. 1), formed between the prosoma and opisthosoma distally and running obliquely posteriad, begins at the distal point of the prosomalopisthosomal articulation and is bounded anteriorly by the recurved "cheek" (gena) of the prosoma. The posterior margin of the channel is formed by the anterior distal margins of the fused segment 9 on the opisthosoma, and the opening is roofed over for approximately one-half its extent by the opercular pleurite. This channel is the main outlet for sand pushed back by the walking legs; the specialized sixth walking leg is modified for pushing sand back through this channel and can be extended all the way through the channel. When forward progress ceases

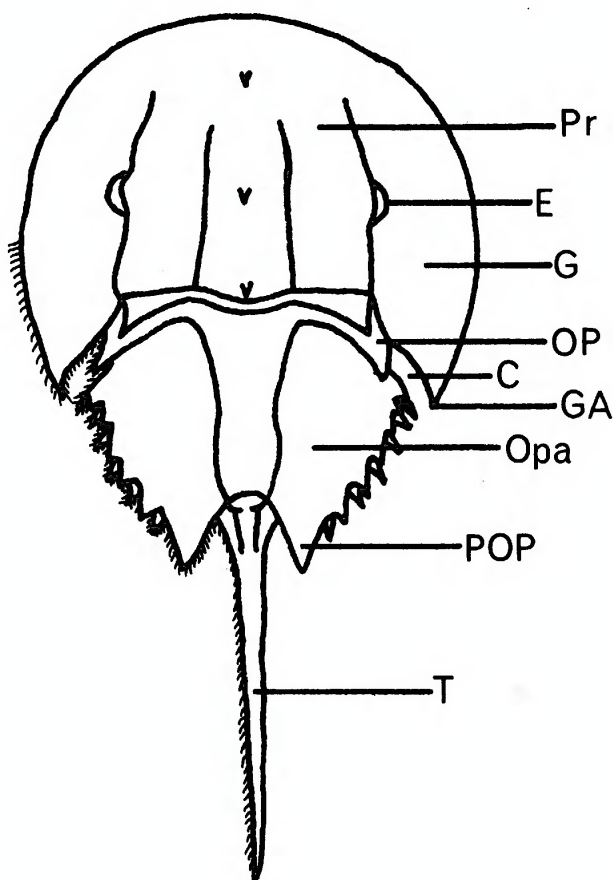


FIG. 1. Anatomical features of *Limulus polyphemus* L. referred to in text.

Abbreviations: C, channel; E, eye; G, gena; GA, genal angle; OP, opercular pleurite; Opa, opisthosoma; POP, posterior opisthosomal projection; Pr, prosoma; T, telson. Distribution of major concentrations of setae shown on left.

in the last moments of Stage 1, the channel is clogged by sand falling through from the top of the carapace. The sixth leg is then used to clear the channel completely both by pushing sand out and away, and also by letting particles collapse into the channel to be removed to another part of the burrow. Stage 1 is completed when clearing of the channel is accomplished and the water current through the channel changes from exhalant to actively inhalant. At this time, the entire prosoma and telson are covered, as well as the anterior one-third of the opisthosoma and its spined margins. One of the rear opisthosomal projections (fig. 1) may also

be covered; if so, the channel on the same side is left clogged. The central medial portion of the opisthosoma is clear of sediment and at least one of the rear projections is left unburied. Stage 1 generally lasts from 30 seconds to about two minutes.

Stage 2, lasting from a few seconds (very rare) to 10 minutes, and normally taking from two to four minutes, is marked by no further burial. All activity is confined to active pumping of water in through the channel and expulsion of the water in about 30 seconds between the telson and the rear opisthosomal projection on the same side as the channel through which the water was taken in. Currents were traced with carmine particles; if both channels and rear opisthosomal projections were exposed, most of the water would be taken in and expelled on one side, although some activity takes place on the other side. The usual case is for one side, seemingly chosen at random, to be buried, leaving the other side clear for water circulation. The apparent reason for this quiescent, water-pumping Stage 2 is a full oxygenation of the opisthosomal gills before final burial.

Burrowing is completed by renewed activity of the walking legs, without downward flexion of the prosoma on the opisthosoma. Sand streams back along the opisthosoma. The rear projection(s) and the central rear portion of the opisthosoma are covered when the animal arches the telson downward posteriorly in the vertical plane, thus raising the rear part of the opisthosoma. The anterior portion of the telson is then rapidly lowered to the horizontal plane, forcing the rear part of the opisthosoma down into the substratum, creating a depression and raising a cloud of fine particles which settles over the opisthosoma. This process may be repeated two or three times before burial is complete. Activity ceases when the last posterior opisthosomal projection is covered, even if a small portion of the medial posterior region of the opisthosoma is accidentally left exposed. Both channels are apt to be clogged with sediment during Stage 3; if so, one of the channels is again cleared by the sixth prosomatic appendage. The final result is a low mound barely distinguishable from the undisturbed substrate surface, with a small hole marking the opening of the channel on one side. This fourth stage is one of virtually total inactivity; water is occasionally taken in through the one exposed channel and gently washed back over the gills, but there is no discrete exhalant channel, and respiratory activity is probably at a minimum. The animal can stay in this state for at least 12 hours, and probably much longer. Stage 4 probably represents the normal mode of passing the daylight hours.

THE ROLE OF DORSAL SETAE IN BURROWING

The immediate onset of burrowing behavior of a specimen of *L.*

polyphemus placed on a suitable, well-lit substratum is probably due to negative phototaxis—there are four separate photoreceptor organs on the dorsal side of the prosoma. Nevertheless, some sensory mechanisms must exist that enable the organism to “know” if portions of the opisthosoma and telson, as well as the posterior portion of the prosoma, are buried. The hypothesis was formed that the dorsal setae, fine structures 1-2 mm. in length, are mechanoreceptors and perform the function of keeping the animal “informed” as to the state of burial.

The distribution of the setae, when viewed in conjunction with the pattern of burrowing behavior described above, is in itself rather suggestive that they are connected in some manner with the burial process. Figure 1 summarizes their distribution; they are restricted to the margins of the carapace and occur as follows: all along the ridge on either side of the telson, along the margins of the posterior opisthosomal projections, and along the margins of both the posterior “cheek” projections (genal angles) of the prosoma, and the opercular pleurites (i.e., the margins of the channel). Setae occur more sparsely between the spines on the medial margins of the opisthosoma and along the posterior ventral portion of the prosomal cheek, where they are continuous with the setae in the channel. The telson is the one organ that is continuously buried from the very beginning of Stage 1. The rear opisthosomal projections are important as exhalant “organs” (see above) and when the last one is finally buried in Stage 3, any medial portion of the opisthosoma that had not received a cover of sediment remains exposed. Final covering of the last posterior opisthosomal projection thus seems to be the signal for cessation of burrowing activity. The role of setae lining the channel is less predictable as current production is an important ongoing function and sensory mechanisms may be more complex and involve ventral organs.

Preliminary tests involved careful uncovering of selected parts of individuals. Results were inconclusive as the possibility of escape reactions precipitated by any general disturbance must be taken into account. However, if any dorsal nonsetae-bearing region of the carapace was exposed, the animal did not rebury. When the telson was entirely exposed, it was immediately brought down with force back into the substratum. Both exposure of the rear opisthosomal projections and widening of the channel to expose the setae precipitated reburial activity, although the reaction rate depended to a large extent on how recently primary burial had occurred. Animals buried for several hours reacted rather sluggishly, whereas animals exposed immediately following the final resting stage reburied quickly.

The hypothesis was further tested by complete cementation of the setae

to the carapace in certain regions; should the setae be tactile sensory organs important in burial, the constant stimulation provided by cement should disrupt the normal function and perhaps result in nonburial of the treated organ or area.

The telson of specimen No. 1 was painted with dental cement and placed back in the tank, where Stage 1 of burial began immediately. The telson was not covered, although it was moved in the normal side-wise manner. At the end of Stage 1, the telson remained uncovered, a condition never seen in untreated organisms. The telson was eventually covered passively simply by being dragged through the substratum and receiving some sediment off the rear of the opisthosoma. Upon exposure, the telson was left on the surface of the substratum; the hypothesis seems clearly confirmed in this case.

Results of covering the setae on the posterior opisthosomal projections on one specimen and the channel setae on another are less straightforward. Specimen No. 6 was chosen for treatment of the posterior projections of the opisthosoma. Burial was abnormal in that at the end of Stage 4, the open channel was on the left side, and the right posterior opisthosomal projection was uncovered, and no active water transport occurred. Such asymmetry and absence of water transport indicates that this was truly Stage 4, and not Stage 2, and that the animal was finished with burrowing. After a lag of 15 to 20 minutes, however, the animal finally covered itself completely by moving forward, not flapping the opisthosoma up and down. It seems quite likely that the cement covering was incomplete or for some reason did not completely simulate burial sensations.

Similarly, when the channel setae of specimen No. 5 were coated, the exhalant channel was left with the setae-bearing portions of the carapace exposed, but otherwise burial was normal. That is to say, some, rather than no, carapace material in the channel area was left exposed. Again, after a long time, simple movement forward eventually covered up the specimen entirely and the normal postburial condition was achieved.

Finally, all three areas were covered over in specimen No. 5. Normal burial progressed, although the carapace around the right channel and the right posterior opisthosomal projection was left uncovered for a much longer period of time than usual. Results, in other words, were exactly comparable with the experiments in which the three areas were treated separately. However, during one test, specimen No. 5 met an obstruction (the side of the aquarium). The dorsal photoreceptors and most of the prosoma were covered, and all other areas, including the

telson, were exposed. Burial ceased completely, and the animal remained exposed for about 20 minutes, a condition never observed in any untreated specimen (normal specimens merely turn when an obstruction is met). Eventually, after the long, abnormal exposure, the animal turned and completed burial.

DISCUSSION OF THE ROLE OF SETAE IN BURROWING

The experiments show that the setae probably are mechanoreceptors functioning as indicators of burial. What remains to be determined is how crucial they are to the burial process. Nothing remotely resembling total disruption of burial was obtained except in the case of the specimen that ran up against the aquarium wall. The burial process as described above is actually a fairly rigid, complicated chain of events, with a precise sequence that must be followed. The establishment of an active water current system during Stage 2, for instance, is a complicated piece of behavior undoubtedly involving ventral sensory mechanisms. After a period of active gill aeration, the next step in the behavioral chain is to move forward and bury the opisthosoma, stopping only after the one remaining posterior opisthosomal projection is covered. It is reasonable to suppose, therefore, that whatever the function of the setae, the burial process in a treated specimen would continue up to the stage immediately preceding final covering of the projection. This was observed to some extent, although total burial eventually did occur. Incomplete disruption may be due to incomplete coating with cement, flaking off of portions of the coating, or some physiological acclimation which regained some of the sensory properties of the setae. The experimental results, as well as the distribution of setae in light of the burial procedure, make it quite likely that the setae are mechanoreceptors that are used in detection of position in burial.

THE ROLE OF PROSOMAL MORPHOLOGY IN BURROWING

A feature of particular interest in *Limulus* is the arcuate bend of the anterior prosomal margin ("anterior arch", Clarkson, 1966a, p. 27) when the dorsal margins of the eyes and the top central portion of the prosoma are oriented in the horizontal plane (fig. 2A, B).

Swimming was not observed in the specimens of *Limulus* kept at the Bodega Laboratory. The frontal arch could conceivably be of use in walking on the substratum to clear obstacles and particularly to bring sense organs and eventually grasping limbs into play should the obstacle

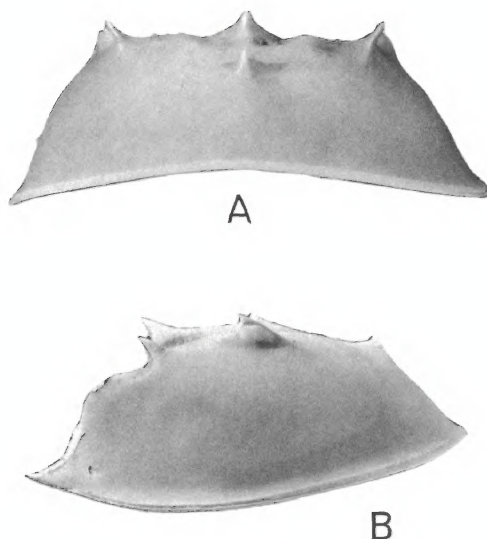


FIG. 2. *Limulus polyphemus* L., specimen No. 5, A.M.N.H. No. 29007. A. Frontal view of prosoma showing anterior arch. $\times 8$. B. Right lateral view of prosoma showing the curvature of the ventral prosomal margin. $\times 8$.

turn out to be edible. The best explanation for both the frontal arch and the high angle of slope to the cephalic margins is probably to be found in the burrowing mechanism, however.

The essential point is that the predominant function of the legs in burrowing is the usual promotor-remotor motion of normal walking and not active excavation of a trough. The downward component is supplied by tilting the prosoma down and walking straight ahead. To be sure, some sediment is displaced by the legs as resistance is met by the external anterior region of the prosoma, but the primary function of the legs is to provide forward thrust.

When *Limulus* walks on the surface, the eyes and top central portion of the prosoma are kept nearly horizontal. To initiate burrowing, the prosoma is flexed downward roughly 15 degrees, which eliminates the frontal arch; in fact, the anterior half of the ventral margin now rests directly on the substratum. Progression forward drives the anterior margin of the prosoma into the substratum. Were there no frontal arch (and the animal could somehow avoid digging in each time it moved forward), the frontal profile would be convex downward when flexed and would create a drag. With the arch, the immediate edge that cuts through the sediment is flat and knifelike when the prosoma is flexed.

The steep angle on the margins of the prosoma creates a thick pile of sand with a minimum amount of distance to travel. The thick layer spreads out over the top of the prosoma and portions of the opisthosoma as described above. Thus with nothing but simple walking legs and a specialized cephalic morphology, *L. polyphemus* can effectively create a burrow in a small area, and rivals other arthropods with more elegant appendages modified for burrowing.

FUNCTION OF COXAL EXITE OF THE SIXTH PROSOMAL APPENDAGE

The small, semicircular structure arising from the distal portion of the coxa of the sixth prosomal appendage, and here termed an exite, following Manton (1963), is situated just anterior to the channel described above and though movable, frequently terminates at the anterior edge of the prosomal margin of the channel. This creates a concave barrier which suggests that water entering the channel and moving anteriorly is deflected back over the gills. The usual function attributed to the exite is gill cleaning (e.g., Lochhead, 1950), although apparently this has never been directly observed, and the exites are quite possibly too short to reach the most posterior gills.

The exites were removed from a specimen. No profound disruption of normal water currents (Stage 2) was observed, but there was less rigid control of the current entering one side to remain on the same side as it was expelled in the rear. It appears, however, that the exites, whatever their relation to gill cleaning may be, are also involved in proper maintenance of water currents used in gill aeration during the burrowing process.

IMPLICATIONS ON TRILOBITE FUNCTIONAL MORPHOLOGY

The relict and primitive nature of *Limulus polyphemus* has been stressed repeatedly; less widely appreciated are the behavioral and anatomical specializations which, combining to form the burrowing mechanism, are highly developed and seemingly quite efficient. Yet burrowing is but a single facet of the panoply of activities in the daily routine of life of *Limulus*, and there is no indication that it performs its other functions any less well. *Limulus* is an object lesson in what can be done, given a morphology essentially "primitive," or basically unelaborated over the ancestral condition.

Delo (1935, p. 406) argued that attached sessile gastropods (chiefly *Crepidula fornicata* L.), barnacles, and mussels "could not have adhered to the test and there attained considerable size if the *Limulus* habitually burrowed beneath the surface." He, and other workers, have also claimed

that the eye in phacopid trilobites was too large and delicate an organ to withstand repeated burial. Although the daytime behavior of large specimens of *Limulus* remains in question, the negative phototaxis displayed by small tank specimens corroborates the belief that smaller specimens, at least, remain passively buried during daylight hours. The same sessile organisms seen adhering to larger carapaces are also commonly observed on smaller, actively burrowing specimens. It is also difficult to consider the eyes of *Limulus* to be any less delicate and susceptible to injury than the eyes of phacopids. The essential point of confusion seems to be that burrowing in *Limulus* is confined to immediate burial, which entails relatively little forward movement entirely beneath the substrate; once the carapace has been totally covered, forward progress stops. Forward locomotion, other than swimming, is accomplished either by walking entirely on top of the substratum surface, or perhaps by plowing forward with the eyes and most of the rest of the carapace exposed. Thus the argument that the large conical eyes of trilobites, like *Dalmanites* Barrande, are not "adapted to slipping easily through the mud" (Delo, 1935) is not valid if a burial behavior based on that of *Limulus* is envisioned for those trilobites.

Many trilobites possess features that have been interpreted as adaptations for burrowing. A partial list of such features includes blindness, development of immovable "eye stalks," development of a shovel-shaped "plow" on the anterior margin of the cephalon, loss of glabellar segmentation, and loss of trilobation. Homalonotids, for example, show not one but all of the above characters with the exception of blindness, although the eyes are very small in relation to total body size. But observations on *Limulus* suggest that characters such as the anterior arch and even perhaps dorsal setae may also be indicative of burrowing, where "burrowing" is defined as quiescent burial during a portion of the day.

THE ANTERIOR ARCH

Clarkson (1966b), in his discussion of "*Phacops*" *musheni* Salter, argued that the most likely orientation of the cephalon in life was with the dorsal margin of the visual surface in the horizontal plane. This conclusion is based on his studies of the physiological implications of lens arrangement in "*P.*" *musheni* and seems to be applicable to phacopids in general. When the cephalon of any of the Phacopina is oriented in this manner (fig. 3A, B), an anterior arch is developed exactly comparable with that of *Limulus*. Indeed, an anterior arch seems to have been characteristic of most trilobites.

Clarkson (1969) has recently presented a detailed analysis of the functional anatomy of the odontopleurid trilobite *Leonaspis deflexa* (Lake). Within this study occurs the only detailed consideration given to the functional implications of the anterior arch yet to appear. Clarkson identified an "active stage," in which the cephalon is tilted forward and the anterior margin of the cephalon is in contact with the substratum, and a "resting stage," in which the head is rotated back some 25 degrees and rests on the posterior lateral margins of the cephalon and the lowermost part of the genal spines. In this "resting stage," the anterior arch is well developed. Clarkson's detailed arguments on the mode of life of this odontopleurid are compelling, and it only remains to point out that the "resting stage" may perhaps better be viewed as the normal walking orientation. Quite apart from the issue of burrowing, by analogy with

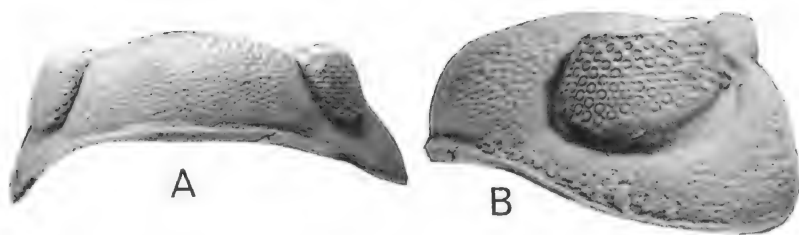


FIG. 3. *Phacops rana crassituberculata* Stumm, A.M.N.H. No. 28898, Silica shale, north quarry, Medusa Portland Cement Company, at Silica, Ohio. A. Frontal view of cephalon showing anterior arch. $\times 2$. B. Left lateral view of cephalon. $\times 3$.

Limulus, *Leonaspis* could hardly avoid digging into the substratum if it attempted to walk forward without an anterior arch. It seems quite likely that most, if not all, trilobites that actively walked on the substratum possessed an anterior arch for this reason.

Although the presence of an anterior arch does not automatically imply burrowing (the spinescence of *Leonaspis*, e.g., argues against burrowing), nevertheless, the simple burrowing mechanism of *Limulus* was probably employed by many trilobites generally considered unlikely candidates for such activity. The blunt anterior cephalic border of *Phacops* Emmrich, for example, has been cited as a hindrance to burrowing (e.g., Delo, 1935, p. 408). Yet the steep anterior slope and the flat inner dorsal surface of the glabella (fig. 3) are very reminiscent of the prosomal morphology of *Limulus*, so much so that it seems quite likely that *Phacops* was able to create shallow resting burrows. The full implications of the anterior arch in *Limulus* on the interpretation of similar struc-

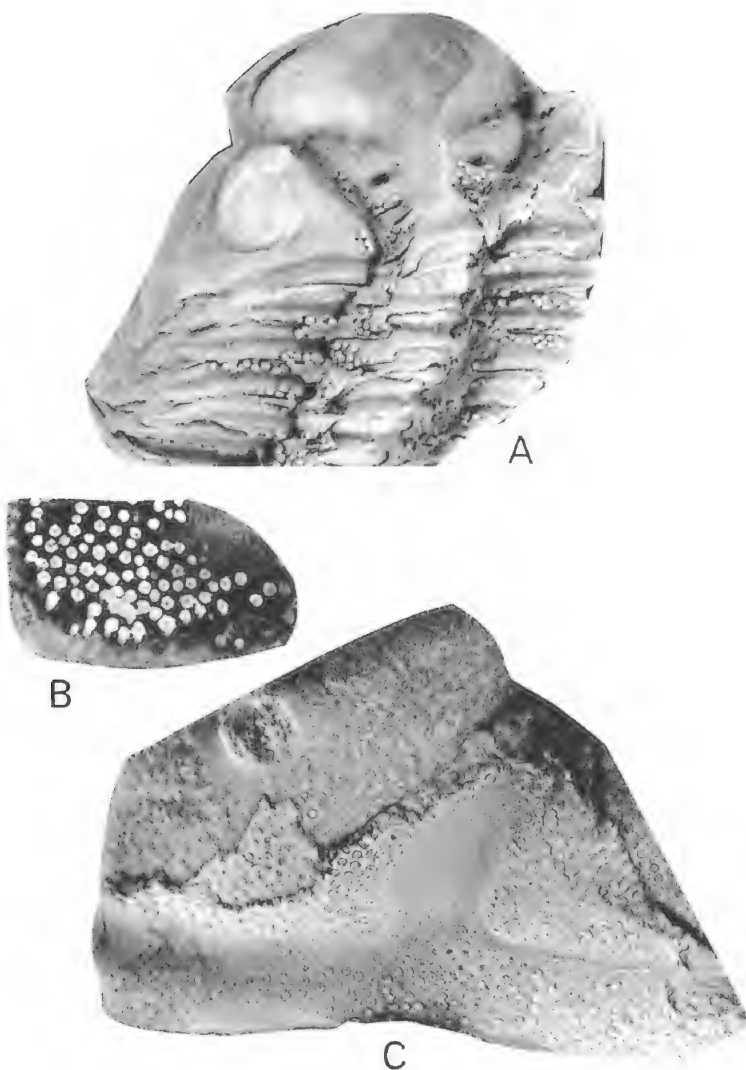


FIG. 4. A. Internal mold of *Greenops boothi* (Green), A.M.N.H. No. 29008, Ludlowville Formation, approximately 2 miles west of Randallville, N. Y. Note sedimentary infillings of carapace canals. $\times 4$. B. External mold of the glabella of *Trimerus (Dipleura) dekayi* (Green), A.M.N.H. No. 29009, same horizon and locality as specimen 4A. Infillings of carapace canals are preserved as rods of sedimentary matrix. $\times 3$. C. Left posterior portion of a cephalon of *Trimerus (Dipleura) dekayi*, A.M.N.H. No. 29010, Ludlowville Formation, 3.6 miles south of intersection of Bradley Brook road and N. Y. route 26, near Eaton, N. Y. The entire area of intact carapace is riddled with canals with the exception of the paraglabellar area. In exfoliated areas, the impressions of the sedimentary infillings can be seen on the internal mold. $\times 2$.

tures in trilobites necessarily awaits functional anatomical studies on single species on the detailed level presented by Clarkson (1969).

DORSAL SETAE

Canals piercing the carapace are known in many trilobites, although detailed histological examination has been performed on very few species. Three general types of canals are recognized in modern arthropods (Richards, 1951); the minute pore canals are concerned with the production of the cuticle. The other two are gland ducts and canals for the attachment and innervation of setae. Although exact identification of the function(s) of perforations in trilobite tests awaits a complete histological survey using scanning and transmission electron microscopy, a few generalizations about trilobite microstructure can be made at present.

Canals of two or three different size (diameter) classes are frequently observed on a single specimen. In *Phacops rana* (Green), the entire carapace is riddled with what seem to be minute pore canals (see Rome, 1936), whereas larger tubules occur on the margins of the cephalon, including the thickened ridges on both sides of the vincular furrow, and the rear margin of the occipital ring. In larger specimens, these larger tubules are also seen on the palpebrum, especially along the facial suture.

Still larger canals have been documented in the Dalmanitacea, and are easily seen under low magnification in examples, such as *Greenops boothi* (Green) (fig. 4A). Although Esker (1968) has claimed the existence of melanopores in both *Greenops* and *Phacops*, it is also possible that these tubules supported the bases of tactile setae.

Tubules are perhaps best known in the Cheiruridae (Evitt, 1953, on *Ceraurus* Green), Calymenidae (Evitt and Whittington, 1953, on *Flexicalymene* Shirley), and Homalonotidae (fig. 4, B, C); all these trilobites also possess an anterior arch. The homalonotids are thought to have been almost assuredly burrowers (see Sdzuy, 1957, for the most recent discussion of the mode of life of homalonotids). In short, some of the tubules piercing the carapace in many trilobite taxa probably represent sites of attachment of dorsal tactile setae, and taken in conjunction with the presence of an anterior arch, may indicate some sort of burial activity on the part of those trilobites.

Certainly more work in functional consideration of cephalic design and histology of the entire carapace remains to be done. But we may conclude that there is already sufficient evidence to suggest that many trilobite taxa were able to excavate shallow burrows and to become buried completely under a thin layer of substratum, despite the seeming absence of structures conventionally cited as evidence of burrowing activity.

SUMMARY

The functional morphology of burrowing was investigated in *Limulus polyphemus* with particular attention paid to the role played by the dorsal setae and prosomal shape.

The burial process can be broken down into four discrete stages. Stage 1 involves active burial by downward flexion of the prosoma and a promotor-remotor swing (normal walking) by the prosomal legs. Sand is forced over the prosoma and anterior one-third of the opisthosoma, and a channel between these two structures is kept clear. Stage 2 involves no further burial, but rather active intake of water through one or both channels, deflection of the current back toward the gills underneath the opisthosoma, and expulsion of the current under one or both posterior opisthosomal projections. Stage 3 is the final burial phase and is effected both by forward walking and forceful flapping of the opisthosoma into the substratum; burial ceases when the last posterior opisthosomal projection is finally buried. The telson is covered throughout this process. Stage 4 is a long period of dormancy.

The dorsal setae, distributed on the margins of the carapace, are mechanoreceptors that aid in keeping the organism buried. Their action is integrated with all other anatomical and behavioral aspects of burrowing, so that burrowing cannot be entirely disrupted by suppression of the tactile setae.

Prosomal shape is at least partially explicable in terms of burrowing efficiency. The frontal arch is a necessary concomitant to a mode of burrowing that utilizes only normal promotor-remotor (walking) activity of the appendages; the arch effectively presents a horizontal edge to the substratum upon flexure of the prosoma of approximately 15 degrees. The high angle of slope of the margin of the carapace creates a thick wall of sediment that covers the rest of the body and allows burial within a minimum amount of space.

The coxal exite of the sixth prosomal appendage is a curved structure that probably deflects the current of water entering at the channel back toward the opisthosomal gill appendages, although they do not carry out this function alone. It may or may not be used to clean the gills, which is the function usually attributed to it.

Limulus polyphemus possesses many anatomical similarities with trilobites. Detailed knowledge of the functional morphology of *L. polyphemus* may, if carefully applied, serve as a model for interpretation of trilobite morphology hitherto incompletely understood. In particular, the nature and role of the sensory dorsal setae and the functional aspects of the

anterior arch in *L. polyphemus* appear to have a direct bearing on interpretation of closely comparable structures in certain trilobites.

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